THE GIRDLES AND LIMBS OF THE GORGONOPSIA OF THE *TAPINOCEPHALUS* ZONE

By

Lieuwe Dirk Boonstra

South African Museum, Cape Town

(With 11 figures in the text)

Contents

Introduction

From the *Tapinocephalus* zone twelve gorgonopsian species have been described, each based on a single specimen, the number of genera being eleven. Of these eleven Watson has put eight into five separate families with the remaining three uncertain as to family. Only six species are based on adequate skulls. Hitherto the postcranial skeleton in only one specimen has been described.

In the South African Museum we have eighteen specimens and of these parts of the girdles and limbs are present in only six specimens.

Material

Specimens with parts of girdles and limbs preserved are:

S.A.M. 8950. *Hipposaurus boonstrai.* Holotype.
  Skull and most of the skeleton much damaged in preparation by a labourer under direction of S.H. Haughton.
  Klein-Koedoeskop, Beaufort West, Low *Tapinocephalus* zone. Collected Boonstra 1928.

S.A.M. 9012. Gorgonopsian.
  Isolated proximal end of a femur.
  Klein-Koedoeskop, Beaufort West.
  Low *Tapinocephalus* zone. Collected Boonstra 1929.

S.A.M. 9081. *Hipposaurus major.* Holotype.

Skull, incomplete pectoral and pelvic girdles, distal end of front epipodial and incomplete manus.

Klein-Koedoeskop, Beaufort West.

Low *Tapinocephalus* zone. Collected Boonstra 1929.

S.A.M. 9084A. ?*Hipposaurus major.*

An isolated humerus lacking the proximal head.

Rietkuil, Beaufort West. Low *Tapinocephalus* zone.

Collected Boonstra 1929.

S.A.M. 12010 Galesuchid?

Bloemhof of Voëlfontein, Prince Albert.

Low *Tapinocephalus* zone. Collected Boonstra and Zinn 1956.

S.A.M. 12118A. Galesuchid.

Part of pelvis associated with a snout.

Palmietfontein of Kruidfontein, Prince Albert.

Low *Tapinocephalus* zone. Collected Boonstra and Zinn 1957.

PECTORAL GIRDLE

(Figs. 1 and 2)

In the two species of *Hipposaurus* the two specimens have the pectoral girdle adequately preserved, but in neither is the cleithrum and in only one is the ossified sternum preserved in part.

The coraco-scapula is well developed with the scapular blade lying at right angles to the vertebral axis but curving slightly around the thorax. The coracoidal plate is large and long and rests on the interclavicle. There is no supraglenoidal buttress or foramen. The scapular facet of the glenoid faces downwards and backwards and slightly outwards.

The coracoidal facet faces upwards and slightly outwards. The precoracoid forms the anterior corner of the glenoid. Immediately anterior to the glenoid, but in a slightly higher level, the precoracoid is pierced by a fairly large foramen supracoracoideum.

Above the glenoid on the posterior edge of the scapula is an indistinct scar for the origin of the scapular head of the triceps muscle. The coracoid is without a process or even a scar for the origin of a coracoidal head of the triceps.

The dermal clavicular girdle is well developed, except the cleithrum which was apparently a slender splint-like bone judging by the facet on the anterior edge of the scapular blade.

The interclavicle is well developed with a broad spatulate anterior expansion curving slightly upwards, a constricted waist and a fairly long and broad tongue-like posterior part.

The anterior spatulate end is underlain in its lateral part by the broad ventral end of the clavicula, which ends well away from the middle line and
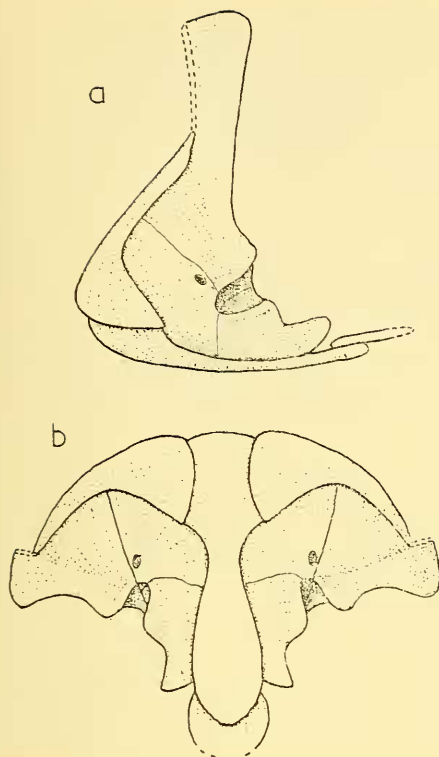
Fig. 1. *Hipposaurus boonstrai. Holotype. S.A.M.*
8950.
Pectoral girdle × ⅓. *a.* Lateral. *b.* Ventral
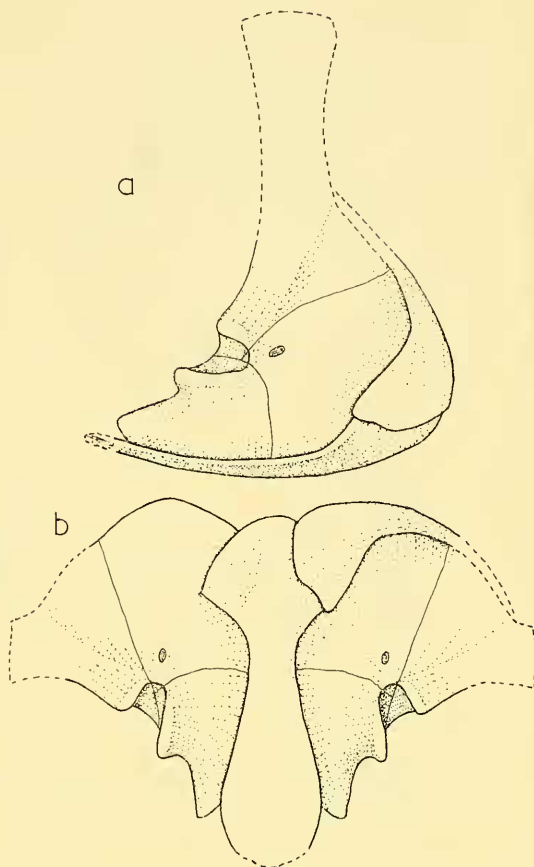
Fig. 2. *Hipposaurus major*. Holotype. S.A.M. 9081.
Pectoral girdle × ⅓. *a.* Lateral. *b.* Ventral.

which has no posteriorly directed process to underlie the interclavicle in posterior direction as is the case in the pristerognathid clavicle.

From its broad, ventral expansion the clavicle sweeps upwards with a rather slender process lying externally and extending slightly anterior to the curved anterior edge of the scapulo-coracoid. Its upper extremity is applied to the anterior scapular edge, where it also meets the ventral end of the cleithrum.

The sternum is ossified as a flattish disc-like element lying above the posterior end of the interclavicle. No facets for the ribs can be seen.

Pelvic Girdle

(Figs. 3 and 4)

The two specimens of the two species of *Hipposaurus* have the pelvic girdle preserved in part. In both the iliac blade is poorly preserved, but the
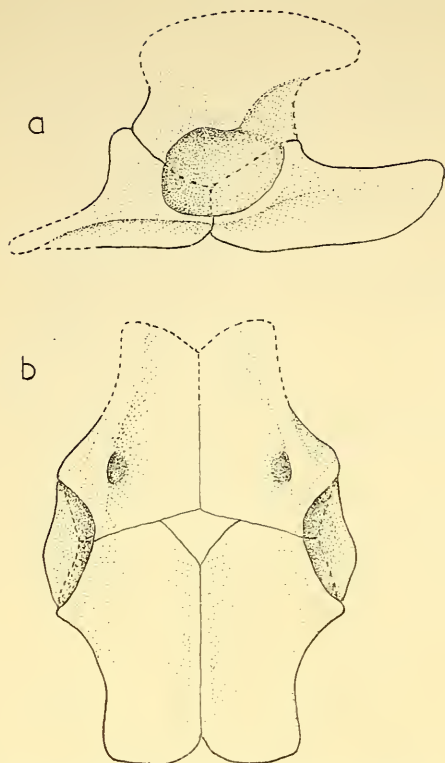
Fig. 4. Galesuchid. S.A.M. 12118 A. Pelvic girdle × ⅓. *a.* Lateral *b.* Ventral.

Fig. 3. *Hipposaurus major*. Holotype. S.A.M. 9081. Pelvic girdle × ⅓. *a.* Lateral. *b.* Ventral

two ventral elements are adequately represented. Associated with a snout identified as a galesuchid species there is the left half of a pelvis with a damaged iliac blade, a good pubis and an incomplete ischium.

From this inadequate material it would appear that the oldest gorgonopsians of the *Tapinocephalus* zone had a low, long pelvic girdle, flattish in its pubic part and V-shaped in its ischiadic part.

The ilium was apparently low. Its blade has little or no anterior process, but with a well developed long but low posterior process. The supra-acetabular edge is sharp with only a weak supra-acetabular buttress, but with a distinct supra-acetabular notch.

The ilium forms about half of the large outwardly facing acetabulum.

The pubes form a flat pelvic floor, long but not very broad. The pubic tubera are weakly developed, but the lateral edge in *Hipposaurus* is strong and girder-like. Each pubis is pierced by a fairly large foramen lying some distance anterior to the posterior pubic edge, facing ventrally it is obscured in lateral view by the girder-like thickened outer pubic edge. Ventrally the two pubes do

not form a keel, where they meet in the median line. In the median line a diamond-shaped lacuna separates the pubes from the ischia.

The ischia meet in the middle line as a strong symphysis forming a well developed ventral keel. Together they are broader than the pubes and also longer. The postero-lateral corners, although thickened, are hardly tuber-like. The ischium forms a strong posterior rim to the acetabulum.

THE HUMERUS
(Figs. 5 and 6)

In the holotype of *Hipposaurus boonstrai* there is a good complete right humerus and the distal end of the left humerus. In addition I have the distal three-quarters of a larger humerus found unassociated with any other part of the skeleton, which I tentatively identify as that of ?*Hipposaurus major*.
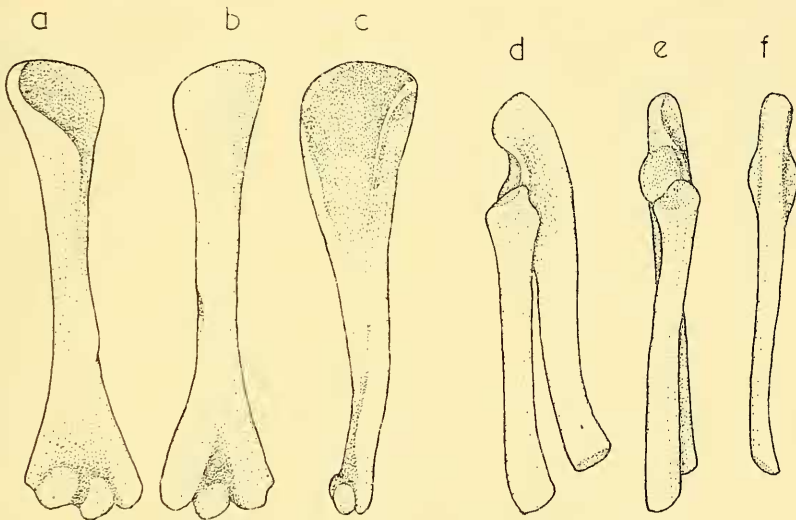

Fig. 5. *Hipposaurus boonstrai*. Holotype. S.A.M. 8950.
Humerus × ⅓. *a*. Ventral in orthoprojection on the distal expansion. *b*. Dorsal in orthoprojection on the distal expansion. *c*. Posterior in orthoprojection on the distal expansion.
Ulna and radius × ⅓. *d*. Anterior. *e*. Median. *f*. Lateral or outer view of the ulna.

The hipposaurid humerus is relatively a long slender bone with a long slender shaft and both the proximal as well as the distal ends moderately expanded. There is a considerable 'twist' on the shaft so that the ends subtend an angle of about 70°.

In the figures the views called dorsal, ventral and posterior are orthoprojections on to the plane in which the distal condyles lie.

The caput is terminal, narrowly oval, flowing into the processus medialis and lateralis, both indistinctly demarcated. The delto-pectoral crest is of moderate size with no distinct pectoralis tuber. The bicipital fossa is deep and

long. The surface for the origin of the medial humeral head of the triceps is well developed. Midway on the shaft there is on the ventral surface a strong ridge lying somewhat posteriorly, flanked by a groove on its postaxial side. This would appear to serve for the insertion of the m. coraco-brachialis longus.

The distal end is remarkable in that no epicondylar foramina are present. In ventral view a longitudinal groove can be seen near the postaxial edge, which is sharp and bent backwards, and this entepicondylar groove housed the median vessels usually passing through the entepicondylar foramen. A similar edge and groove, but of much weaker development on the radial side carried the radial vessels which pass through the ectepicondylar foramen when this is present. Distally the entepicondyle is better developed than the ectepicondyle.
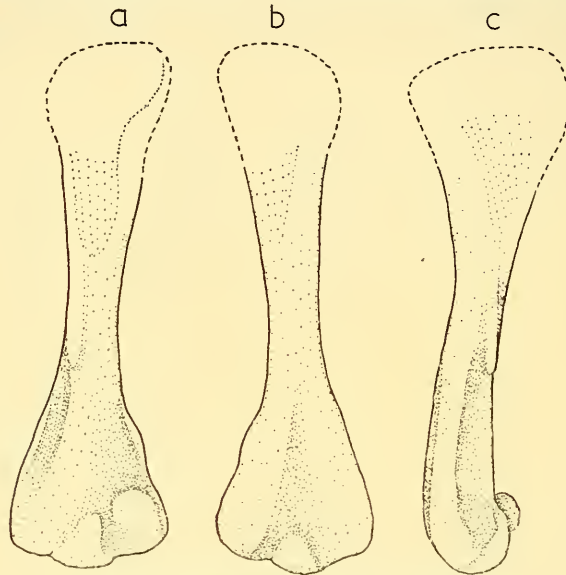

Fig. 6. ?*Hipposaurus major*. S.A.M. 9084A.
Humerus × ⅓. *a*. Ventral. *b*. Dorsal. *c*. Posterior.

Both condyles are well modelled. The radial condyle forms a prominent oval capitellum which faces mostly ventrally. The ulnar condyle lying further distally curves around the end of the bone on to the dorsal surface, where proximally lies a deep, well excavated trochlear fossa. Ventrally the brachialis fossa is very shallow, giving the hipposaurid humerus a quite different appearance from that of the other therapsids where there is a well developed entepicondylar foramen.

THE FEMUR
(Fig. 7)

In the type specimen of *Hipposaurus boonstrai* there are a good right femur and the proximal and distal ends of the left femur. The only additional material

at my disposal is a proximal end found as an isolated fragment and thus only subordinately identifiable.

The hipposaurid femur is a long lightly built bone with very moderately expanded proximal and distal ends. It is sigmoidally curved with the ends subtending an angle of about 30°. The caput femoris is terminal, but through the preaxial curvature on the shaft, it is somewhat preaxially directed. The external trochanter is not very clearly demarcated.

In ventral view the proximal end of the femur is most peculiar.

Halfway along the bone the ventral surface of the shaft has a low curvature in section. In proximal direction in the midline a low ridge becomes progressively developed, with the surface both pre- and postaxially becoming only slightly hollowed out in section. This ridge then ends abruptly with a sharp oblique edge. This ridge representing a remnant of the primitive 'Y'
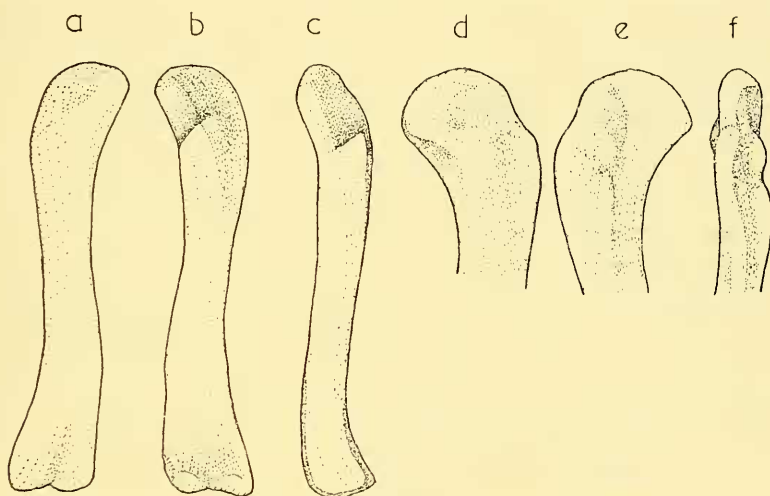

Fig. 7. Femora × ⅓. *Hipposaurus boonstrai*. Holotype. S.A.M. 8950.
a. Dorsal. *b*. Ventral. *c*. Anterior.
Gorgonopsian. S.A.M. 9012A.
d. Dorsal. *e*. Ventral. *f*. Posterior.

system, represents the internal trochanter. Proximal to the internal trochanter the preaxial edge is strongly rounded and postaxially a hollow represents the intertrochanteric fossa. Distally of the internal trochanter there is no indication of a separate fourth trochanteric ridge for the m. coccygeo-femoralis.

On the dorsal proximal surface there is a weak ridge near the preaxial edge for the insertion of the m. pubo-ischio-femoralis internus and externally of this ridge a shallow depression for the insertion of the m. ilio-femoralis. The distal condyles for the reception of the tibia are terminal with the fibula articulating with the outer face of the ectocondyle.

The other gorgonopsian femur available differs considerably from that of the above hipposaurid.

The external trochanter is clearly demarcated and on the dorsal preaxial edge there is a distinct pubo-ischio-femoralis internus ridge flanked by a groove.

On the ventral surface there is a distinct low mound distally of the inter-trochanteric fossa constituting a separate internal trochanter. Distally of this lies a long low ridge to which the m. coccygeo-femoralis was attached and this constitutes the fourth trochanter.

THE ANTERIOR EPIPODIAL
(Figs. 5d, e, and f and 8)

In *Hipposaurus boonstrai* there is a good left and parts of the right epipodial, whereas in *H. major* only the distal ends of the radius and ulna are preserved.

Both radius and ulna are long slender bones. The radius has a well modelled proximal facet, cup-like to fit closely on to the well modelled capitellum of the humerus. On the postaxial corner of the radius there is a well developed flange for the insertion of the biceps. The proximal postaxial edge of the radius fits against the rim of the sigmoid fossa of the ulna.

The ulna is much longer than the radius, with its sigmoid fossa and olecranon process lying proximally of the proximal radial facet.

The sigmoid fossa is formed by the preaxial surface of the olecranon and the proximal surface of the coronoid process. It fits accurately round the trochlea of the humerus to form an efficient hinge-joint.

Proximally of the sigmoid fossa the olecranon carries a very well developed process, broad but dorso-ventrally compressed. In extension this process passes into the deep olecranon fossa on the dorsal surface of the humerus.

In the type specimen of *Hipposaurus major* the distal end of the radius is seen to have a large oval facet for its articulation with the radiale. A similar facet on the ulna articulates with both intermedium and ulnare.

THE MANUS
(Fig. 8)

In 1935 I gave a figure and description of the badly damaged carpus of *Hipposaurus boonstrai*. Now I have the carpus of *Hipposaurus major* prepared by myself with the aid of adequate equipment and from this specimen one gets a better picture of the structure of the hipposaurid carpus.

In the proximal row there are three bones, with an additional large disc-like pisiforme postaxially. The radiale is a stout bone with a large oval proximal facet for the radius and distally a smaller facet for the first centrale. On its curved postaxial surface the intermedium and second centrale are articulated.

The intermedium has a well developed dorsal surface as the bone is not compressed from side to side. Proximally a good oval facet faces the inner part of the distal ulnar facet and a similar facet distally meets the second centrale distally.

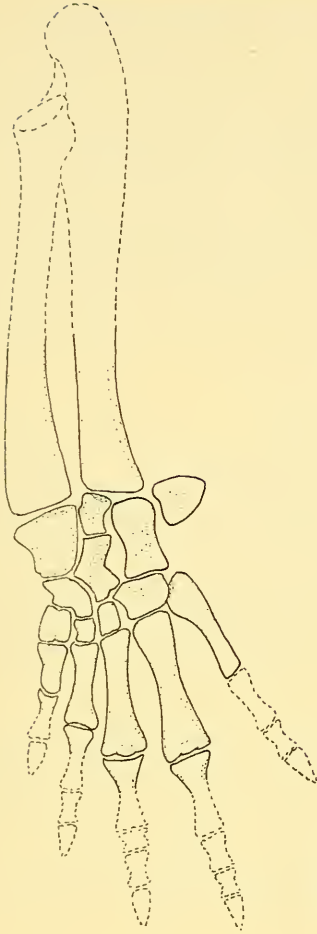The ulnare is an elongated fairly flattened bone with expanded ends and a

Fig. 9. *Hipposaurus boonstrai*. Holotype. S.A.M. 8950 × $\frac{1}{3}$. Hind epipodial.

Fig. 8. Epipodial and manus in dorsal view × $\frac{1}{3}$. *Hipposaurus major*. Holotype. S.A.M. 9081.

slightly constricted waist. The proximal facet is a long oval and distally a similar facet meets the enlarged fused fourth and fifth distal carpals. The first centrale is a curiously shaped bone, distally it has two facets for the first two distal carpals, a proximal facet for the radiale and postaxially a curved face is applied to the concave face of the second centrale. The second centrale is larger, but also curiously shaped with two distal facets, one for the third distal and the other for that part of the fused element constituting the fourth distal. Proximally it has good contact with the intermedium and preaxially two faces fit against the radiale and first centrale respectively.

There are four distal carpals. The first large, the second and third smaller and the fourth a large element representing a fusion of the fourth and fifth.

All five metacarpals are completely and well preserved.

The first metacarpal is the shortest with an expanded proximal end matching the large first distal; but the distal end is unexpanded.

The second metacarpal is longer with both ends expanded and a long constricted shaft.

The third metacarpal is even longer with a well expanded and well modelled distal end.

The fourth metacarpal is the longest bone of the metapodium, with both ends expanded and the distal well modelled.

The fifth metacarpal is of distinctive shape; its proximal end has its facet for the fused fourth and fifth distal directed preaxially and its distal end is not expanded.

Of the digits only the proximal ends of the first four phalanges are preserved.

POSTERIOR EPIPODIAL
(Fig. 9)

The right epipodial is well and completely preserved and the left incompletely in the type specimen of *Hipposaurus boonstrai*. It is composed of two long bones with the tibia fairly robust and the fibula of lighter build. The tibia is a straight bone, but the fibula is much curved so that there is a good spatium interosseum. In the fibula the two ends are expanded with the proximal end the stronger. In the tibia the distal end is only moderately expanded, whereas the proximal end is quite massive. This meets the femoral condyles end on, whereas the proximal end of the fibula is applied in a sliding joint to the postaxial epicondyle.

On its dorsal face the tibia has proximally a strongly developed cnemial crest, which extends far proximally fitting into the intercondylar sulcus of the femur and gives a good surface for the insertion of the tendon of the femorotibialis and associated muscles.

Distally the tibia is applied to the rounded knob-like facet on the astragulus and the fibula to a similar facet on the calcaneum.

THE PES
(Fig. 10)

In the holotype of *Hipposaurus boonstrai* there are a good right pes and parts of the left foot. Since my original description in 1934 I have been enabled by better equipment to expose the tarsal elements more fully. This applies particularly to the astragulus, which is now also visible from the plantar surface.

The calcaneum is most peculiar, but its structure can be easily derived from the typical disc-like element found in most therapsids. In its distal part the calcaneum is typically therapsid and its distinctive shape is due to the additional development of a strong well modelled tuber proximally. Distally the calcaneum has a slightly domed dorsal surface and a broad distal facet for the large conjoined fourth and fifth distal tarsals. Further proximally the dorsal surface carries a strong rounded facet for the fibula. Proximally of this

facet a strong hook-like curved tuber is developed, with postaxially a strong
rounded ridge running from the fibular facet to the extremity of the tuber.
Between this ridge and the fibular facet there is a saddle-shaped excavation.

Preaxially the calcaneum is applied to the astragulus so that the fibular
and tibial facets lie in the same plane as also the distal facets of the two bones.
The cruro-tarsal articulation thus lies in one plane. In plantar view it is seen
that the calcaneum in its preaxial part is overlain by the astragulus.

The astragulus has on its proximal dorsal surface a strong rounded knob-
like facet for the tibia. Distal to this knob there is a deep transverse groove,
with distally a shallowly concave upper surface passing distally into the distal
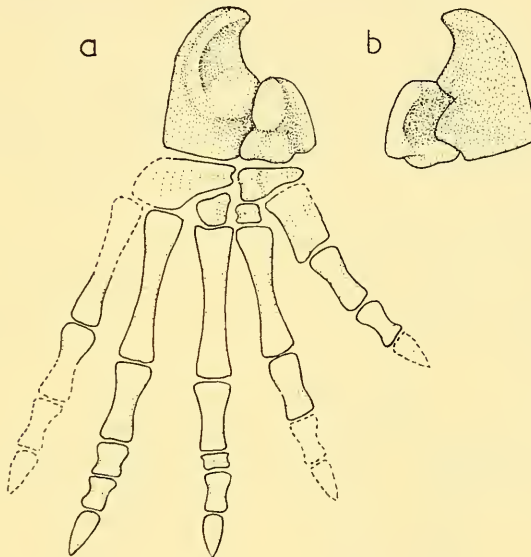facet for the centrale. In my original description I thought that this groove

Fig. 10. *Hipposaurus boonstrai.* Holotype. S.A.M. 8950 × ½.
a. Dorsal view of pes as reconstructed. b. Plantar view of
astragalus and calcaneum.

indicated a line of junction between two formerly separate elements, but the
exposure of the plantar surface does not support this view. Preaxially it can
now be seen, particularly in plantar view, that the astragalus extends further
than shown in my original figure. In plantar view this preaxial extension is
seen to form a strong process with a downwardly directed thick rounded edge.

The single centrale is a peculiar wedge-shaped bone lying transversely
between the astragalus and the first two distal tarsals.

The greatly enlarged fused fourth and fifth distal tarsal has a very similar
wedge shape and lies between the calcaneum and the third distal and articu-
lating with the fourth and fifth metatarsals.

The first distal tarsal is of most unusual shape. It is a large elongated bone looking much more like a shortened metatarsal than a distal tarsal.

The second distal is a small squarish bone articulating with the centrale and the second metatarsal. The third distal is larger and lies between the fused fourth and fifth tarsal and the third metatarsal.

The metatarsals are all long bones with expanded ends and slender shafts, except the first which is quite short.

The phalanges are only completely preserved in the fourth and fifth digits. The phalangeal formula can thus be given as 2, 3, 4, 4, 3.

The second phalanx of the third digit is much reduced and in a near descendant of *Hipposaurus* one can expect a formula of 2, 3, 3, 4, 3 which would later become 2, 3, 3, 3, 3.

In another specimen, S.A.M. 12010, which is in all probability a galesuchid, and prepared for study since the above was written, there are associated with fragments of skull and vertebrae much weathered parts of the limbs, including the proximal part of a tarsus, an ulna and the middle part of a manus. The ulna has its sigmoid face not situated medially, nor does it have the well developed proximal process to the olecranon as in *Hipposaurus*. The ulna thus agrees more with the ulnae as known in later gorgonopsians.

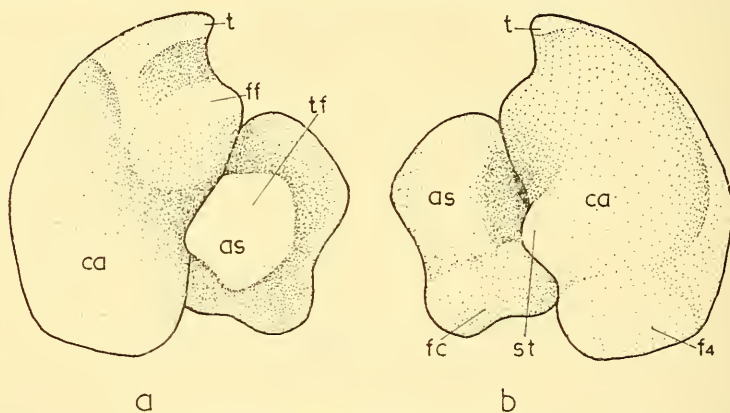The proximal tarsals merit description (fig. 11).

Fig. 11. *Hipposaurid.* S.A.M. 12010 × 1.

The proximal tarsal bones of the left hind foot. *a.* Dorsal. *b.* Ventral.
As — astragalus
Ca — calcaneum
fc   — facet for the centrale
ff   — facet for the fibula
f4   — facet for the fourth distal
t   — tuber calcis
tf   — facet for the tibia.

The calcaneum is a large element which still retains some of the characters of the primitive flattened disc-shaped structure, but in its proximal part shows

highly advanced characters, viz. the facet for the fibula no longer lies proximally but is shifted on to the dorsal surface and protruding backwards it shows a quite well developed tuber separated from the fibular facet by a deep groove.

In ventral view it is clearly seen that the astragalus overlies the calcaneum medially. Here the calcaneum has a well developed process extending under the astragalus and this process can be considered a sustentaculum tali. The gorgonopsians from so low down as the *Tapinocephalus* zone are thus the first therapsids to show this typical mammalian structure.

The astragalus is a much smaller bone than the calcaneum and has a most remarkable facet for the tibia raised well above the base of the bone as a high eminence.

The distal facets of both the calcaneum and astragalus for the fourth distal and centrale, respectively, are very well modelled.

Discussion

A comparative account will be given in a subsequent paper, when I have completed my study of the other therapsids of the *Tapinocephalus* zone.

Summary

Descriptions are given of the girdles and limbs of the Gorgonopsia of the *Tapinocephalus* zone in South Africa. Of the eighteen specimens in the South African Museum, six have parts of the girdles and limbs present, and this account is based on these specimens.

Acknowledgements